THE *PALEORHINUS* BIOCHRON AND THE CORRELATION OF THE NON-MARINE UPPER TRIASSIC OF PANGAEA

by ADRIAN P. HUNT *and* SPENCER G. LUCAS

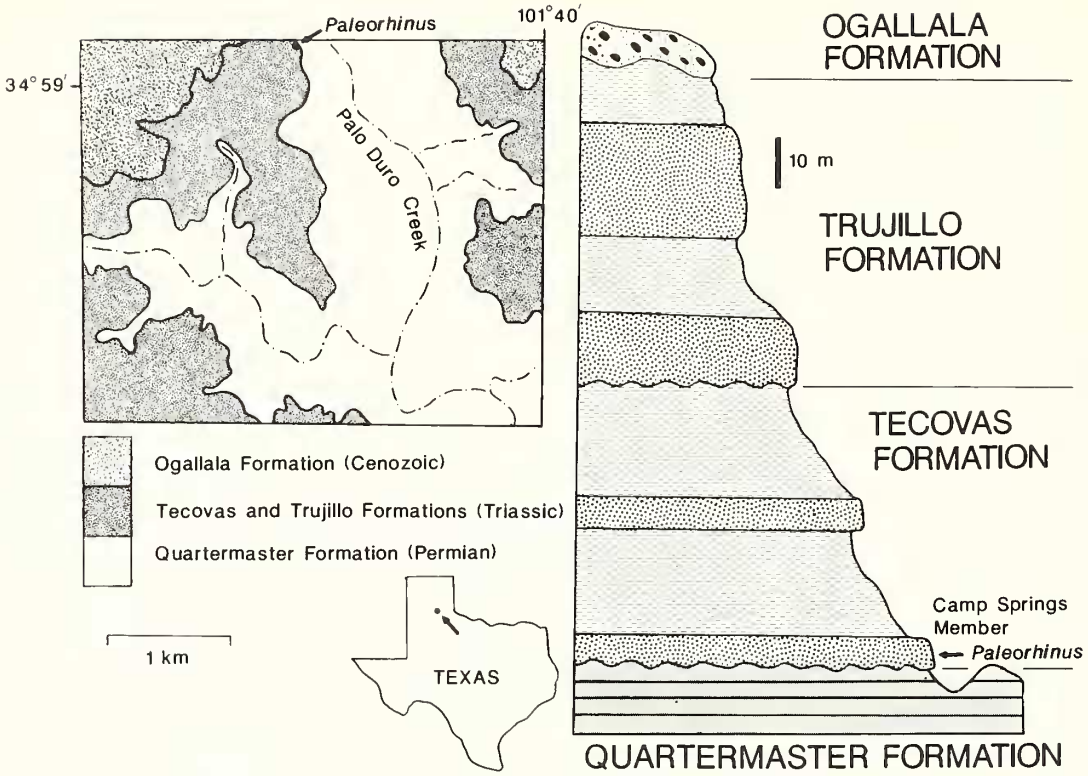
ABSTRACT. We describe a new skull of the phytosaur *Paleorhinus bransoni* from Palo Duro Canyon, Randall County, Texas. The genus *Paleorhinus* (synonyms, *Mesorhinus*, *Promystriosuchus*, *Francosuchus*, *Ebrachosuchus*, *Mesorhinosuchus*, *Parasuchus*) contains four valid species: *P. bransoni* (synonyms *P. parvus*, *P. scurriensis*), *P. neukami*, *P. magnoculus*, and *P. hislopi*. Other nominal species based on specimens that we assign to *Paleorhinus* are *nomina dubia*. *Paleorhinus* is a constituent of late Carnian faunas in the western United States (lower Dockum Group, Camp Springs Member of the Tecovas Formation, lower Chinle Formation, Popo Agie Formation), Germany (Blasensandstein), Morocco (Argana Formation), India (Maleri and Tiki Formations), and Austria (Opponitzer Beds). These faunas, together with correlative faunas which lack *Paleorhinus* in Scotland (Lossiemouth Sandstone Formation) and South America (upper Santa Maria and Ischigualasto Formations), encompass a *Paleorhinus* biochron which can be recognized across much of the Late Triassic of Pangaea. The age of this biochron is based on pollen, marine invertebrates, and radiometric dates.

PALO Duro Canyon in Randall County, Texas (Text-fig. 1) contains one of the most extensive exposures of the Tecovas and Trujillo Formations of the Upper Triassic. These strata have produced abundant vertebrate fossils elsewhere (e.g. Case 1922; Murry 1982, 1989; Chatterjee 1986), but relatively few from Palo Duro Canyon (Schaeffer and Gregory 1961; Schaeffer 1967; Long and Ballew 1985; Murry 1989). These collections include specimens of the phytosaur *Rutiodon* (Murry 1989), but no material of the generally older and more primitive phytosaur *Paleorhinus*. The nearest occurrence of *Paleorhinus* is about 200 km to the south at Home Creek, Crosby County (Case 1922). Here, we report a new occurrence of *Paleorhinus* in Palo Duro Canyon, which reveals a hitherto unknown faunal level in the Upper Triassic of this area. Phytosaurs are long-snouted, semi-amphibious vertebrates which constitute the majority of specimens collected in the Upper Triassic strata of western North America (Camp 1930; Gregory 1962).

The *Paleorhinus* skull from Palo Duro Canyon, Texas was discovered in 1966 by Nick Petruccione and David Hughes, and collection was supervised by Jack T. Hughes, Curator of Paleontology at the Panhandle Plains Museum. The locality is P217 in the locality records of the Panhandle Plains Museum (UTM 3,874,800 m N/ 256,850 m E Zone 14), and it lies just north of the northern boundary of Palo Duro Canyon State Park, on the west side of Palo Duro Creek in Randall County, Texas (Text-fig. 1). The skull was found in a basal conglomerate unit of the Upper Triassic strata, 0·25 m above the Permian Quartermaster Formation (Text-fig. 1), which also includes white sandstone and purple claystone. This conglomerate represents the northernmost outcrop of the Camp Springs Member of the Tecovas Formation, a stratigraphic unit that has yielded a skull of *Paleorhinus* in Scurry County, Texas (Langston 1949).

This article discusses the taxonomic status of the new skull, which necessitates a revision of the genus *Paleorhinus* and a consideration of all specimens assigned to this taxon. The widespread occurrence of this genus and its limited temporal range make it ideal for intercontinental correlation. The final portion of this paper discusses the definition and distribution of a *Paleorhinus* biochron throughout Pangaea.

[Palaeontology, Vol. 34, Part 2, 1991, pp. 487–501.]



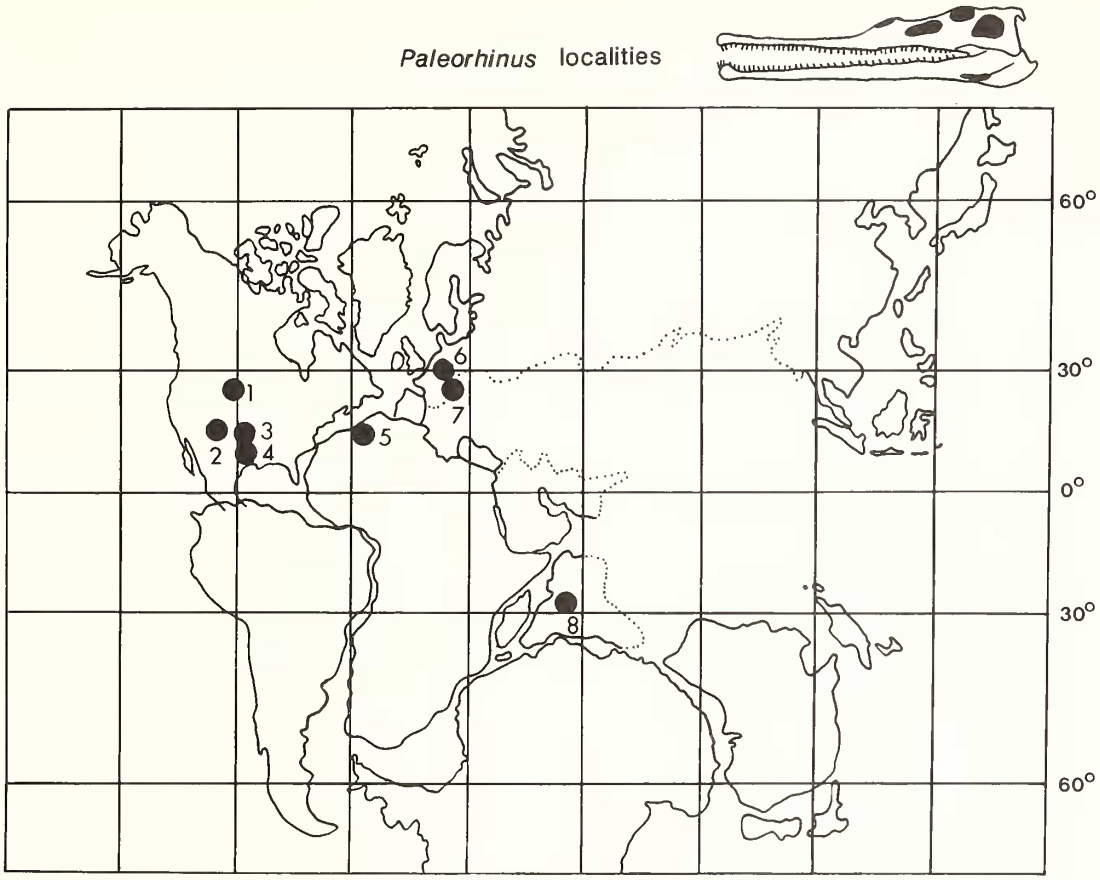
TEXT-FIG. 1. Geological map of part of Palo Duro Canyon, West Texas (after Matthews 1969), and a stratigraphic section showing the *Paleorhinus* locality.

Abbreviations. The following institutional abbreviations are used in this paper: FMNH UC, Field Museum of Natural History, University of Chicago Collection, Chicago, Illinois; MNA, Museum of Northern Arizona, Flagstaff, Arizona; MU, University of Missouri, Columbia, Missouri; NMMNH, New Mexico Museum of Natural History, Albuquerque, New Mexico; PPM, Panhandle Plains Museum, Canyon, Texas; TTUP, Texas Tech. University, Lubbock, Texas; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan; UT, University of Texas, Austin, Texas.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA Laurenti, 1768
Subclass DIAPSIDA Osborn, 1903
Order PSEUDOSUCHIA Zittel, 1890
Suborder PHYTOSAURIA Camp, 1930
Family PHYTOSAURIDAE Lydekker, 1888
PALEORHINUS Williston, 1904

1904 *Paleorhinus* Williston, p. 696, fig. 6.
1910 *Mesorhinus* Jaekel, p. 219, figs 2–6.
1922 *Promystriosuchus* Case, p. 49, fig. 21; Pl. 11A–D.
1932 *Francosuchus* Kuhn, p. 123, figs 5 and 6; Pl. 5, 1 and 2.
1936 *Ebrachosuchus* Kuhn, p. 77, fig. 4–5; Pl. 8, 1a–e; Pl. 10, 1 and 4.
1961 *Mesorhinosuchus* (*Mesorhinus*) Kuhn, p. 79.
1978 *Parasuchus* Chatterjee, p. 86, figs 1–14.



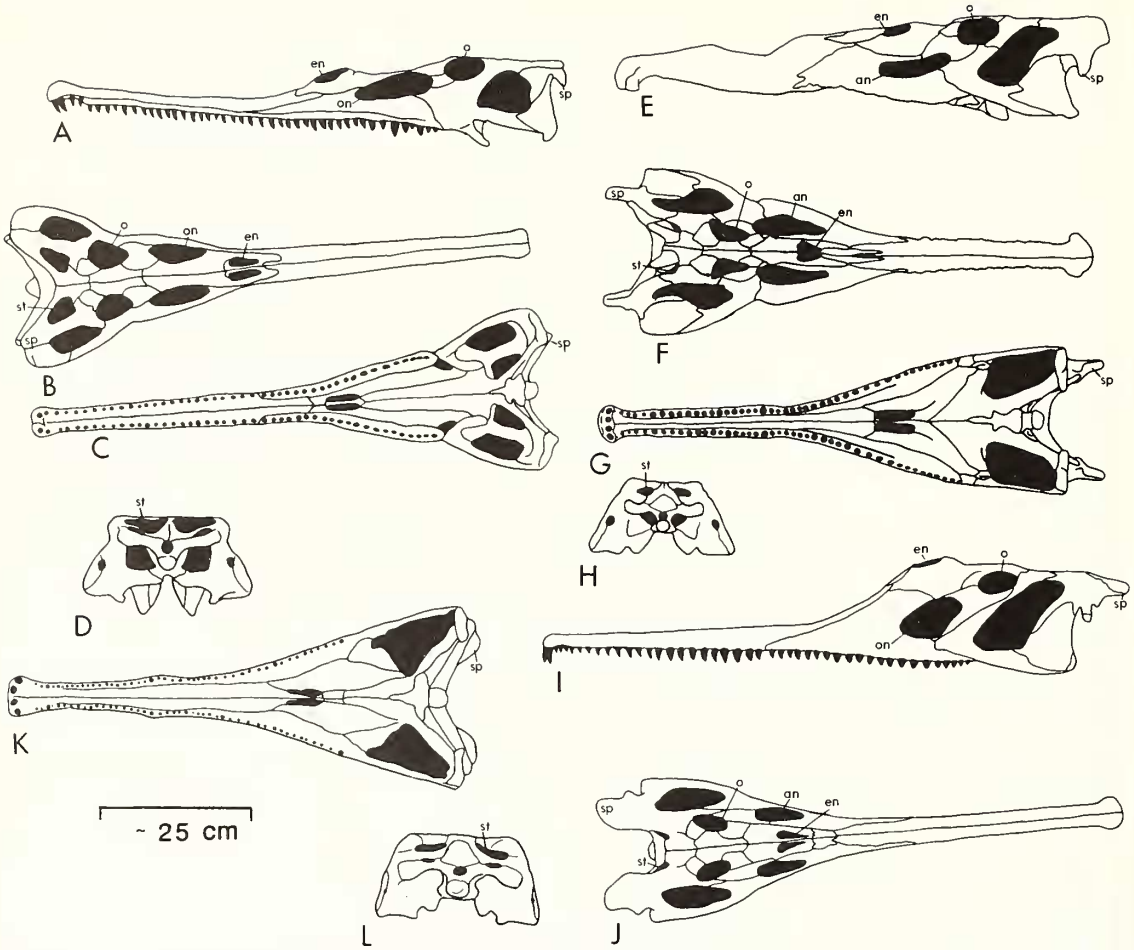
TEXT-FIG. 2. *Paleorhinus* localities of the Late Triassic Pangaean supercontinent. 1, Popo Agie Formation, central Wyoming (USA). 2, lowermost Petrified Forest Member of the Chinle Formation, northeastern Arizona (USA). 3, Camp Springs Member of the Tecovas Formation, Palo Duro Canyon, West Texas (USA; see Text-fig. 1). 4, lower part of undivided Dockum Group, Howard County, Texas (USA). 5, Argana Formation, Morocco. 6, Blasensandstein, West Germany. 7, Opponitzer Beds, Austria. 8, Maleri and Tiki Formation, India.

Type Species. *Paleorhinus brausoni* Williston, 1904.

Included species. The type species and *P. hislopi* Lydekker, 1885, *P. neukami* Kuhn, 1936, *P. magnoculus* Dutuit, 1977. The following named species are based on specimens of *Paleorhinus*, but are *nomina dubia*: *Mesorhinus fraasi* Jaekel, 1910, *Promystriosuchus ehlersi* Case, 1922, *Paleorhinus broilii* Kuhn, 1932, *Francosuchus latus* Kuhn, 1932, *Ebrachosuchus angustifrons* Kuhn, 1936, and cf. *Francosuchus trauthi* Huene, 1939.

Distribution. Popo Agie Formation of Wyoming, lower part of Petrified Forest Member of the Chinle Formation of Arizona, Camp Springs Member of the Tecovas Formation and lower part of Dockum Group (undivided) of West Texas, Blasensandstein (Germany), Opponitzer Beds (Austria), Argana Formation (Morocco), and Maleri and Tiki Formation (India) (Text-fig. 2). All these stratigraphic units are late Carnian (Late Triassic) in age (see later discussion).

Revised Diagnosis. Phytosaurid that differs cranially from others in the following features: external nares lie anterior to the antorbital fenestrae; dorsal margin of external nares is inclined anteriorly; orbits are dorsally oriented; and quadratic foramina are large.



TEXT-FIG. 3. Skulls of the three common genera of Upper Triassic phytosaurs in North America, mid-late Carnian *Paleorhinus*, late Carnian *Rutiodon*, and Norian *Pseudopalatus*. A–D, *Paleorhinus* (after Chatterjee 1978); A, lateral view; B, dorsal view; C, ventral view; D, posterior view. E–H, *Rutiodon*; E, lateral view (after Case and White 1934); F, dorsal view (after Case and White 1934); G, ventral view (after Case 1922); H, posterior view (after Case 1922). I–L, *Pseudopalatus*; I, lateral view (after Camp 1930); J, dorsal view (after Mehl 1928*a*); K, ventral view (after Mehl 1922); L, posterior view (after Mehl 1928*a*). Abbreviations: an, antorbital fenestra; en, external nares; o, orbit; sp, squamosal process; and, st, supratemporal fenestra.

Discussion. *Paleorhinus* is the least derived phytosaur (Ballew 1989) because it has external nares anterior to the antorbital fenestrae and a posterior temporal arcade at the level of the skull roof (Text-fig. 3). The contemporary *Angistorhinus* also has a high posterior temporal arcade, but this genus has more posterior external nares. Phytosaurs of generally younger, Carnian age than *Paleorhinus*, such as *Rutiodon* (Text-fig. 3), are characterized by external nares above the antorbital fenestrae, posteriorly-rounded squamosal processes and a posterior temporal arcade that is wrapped around and under the posterior margin of the skull roof with small supratemporal fenestrae. Norian phytosaurs, such as *Pseudopalatus*, have slit-like supratemporal fenestrae and posteriorly-elongate squamosal processes (Text-fig. 3).

Several genera are here considered subjective junior synonyms of *Paleorhinus* (see above). Later discussion will indicate why we consider the type species of these genera to pertain to *Paleorhinus*.

TEXT-FIG. 4. *Paleorhinus bransoni*, PPM P217, incomplete skull from Palo Duro Canyon, West Texas. A, dorsal view. B, ventral view. C, drawing of dorsal view. Abbreviations: af, antorbital fenestra; f, frontal; j, jugal; l, lachrymal, lf, lateral fenestra; n, external nares; na, nasal; o, orbit; p, parietal; pf, prefrontal; po, postorbital; pof, postfrontal; q, quadrate; qf, quadratic foramen; so, supraoccipital; sq, squamosal; and, st, supratemporal fenestra.

Paleorhinus bransoni Williston, 1904

1904 *Paleorhinus bransoni* Williston, 1904, p. 696, fig. 6.
1928*b* *Paleorhinus parvus* Mehl, p. 142, figs 1 and 2; pl. 37, 1–10; pl. 38, 1–7; pl. 39, 1–2, 4.
1949 *Paleorhinus scurriensis* Langston, p. 325, figs 1–3.

Holotype. FMNH UC 632, skull (Williston 1904, fig. 6; Lees 1907, fig. 1–7).

Locality and Horizon. Popo Agie Formation (Upper Triassic) at Squaw Creek, southeast corner of Township 3 South, Range 1 East, Fremont County, Wyoming.

Referred specimen. PPM P217, a partial skull (Text-fig. 4).

Description of referred specimen. PPM P217 is a phytosaur skull that lacks the rostrum anterior to the external nares and portions of the maxillae lateral to them, and all palatal elements anterior to the posterior portion of the basisphenoid. The maximum length of the skull is 414 mm, with a maximum width of 357 mm, which has been increased by flattening of the skull. The skull is relatively undeformed, although the basioccipital has been pushed forward about 20 mm, and the ventral portions of the quadrates have been pushed posteriorly. The main deformation is the dorsoventral flattening evident in the orientation of the quadrates.

The external nares are well forward of the antorbital fenestrae, as is the case with '*Parasuchus*' *hislopi* (Chatterjee 1978), *Paleorhinus magnoculus* (Dutuit 1977) and *Paleorhinus bransoni* (Lees 1907). The antorbital fenestrae are relatively small. Although the anterior margins of both antorbital fenestrae are broken, the curvature of the upper and lower margins of the right fenestra indicates its original size. In dorsal view, the posterior margin of the skull appears very wide, but this is due to dorsoventral distortion. The external nares are inclined anteriorly. The lateral temporal fenestrae are roughly square in shape and have dorsal margins that are longer than the antorbital fenestrae. The quadratic foramina are large (19 mm maximum diameter) and visible in dorsal view because of the flattening of the skull. The sutural pattern is consistent with other specimens of *Paleorhinus* (e.g. Langston 1949; Chatterjee 1978).

PPM P217 is assigned to *Paleorhinus* on the basis of having external nares anterior to the antorbital fenestrae, external nares whose dorsal margins incline anteriorly, and the possession of large quadratic foramina. This specimen is assigned to *Paleorhinus bransoni* because of the small size of the orbits (cf. *P. magnoculus*) and inclusion of the jugal in the antorbital fenestrae (cf. '*Parasuchus*' *hislopi*: Chatterjee 1978, text-fig. 3*a*). The only morphological difference between *P. bransoni* and *P. neukami* is in the length of the rostrum, a feature not preserved in the new specimen. On the relatively weak grounds of geographic proximity, the new skull is thus identified as *Paleorhinus bransoni*.

PALEORHINUS TAXONOMY AND DISTRIBUTION

USA

Wyoming. Williston (1904) named *Paleorhinus* (type species *P. bransoni*) for a skull from the Popo Agie Formation at Squaw Creek in the Wind River Mountains of western Wyoming (Mehl 1928*b*). Williston (1904) briefly described the genoholotype of *P. bransoni*, and subsequently Lees (1907) described it in detail. Mehl (1915*b*, 1928*b*), Jaekel (1910) and Langston (1949) criticized several of Lees' (1907) interpretations of the structure of the *Paleorhinus* skull, but did not doubt its generic distinctiveness. Mehl (1915*a*, 1915*b*) demonstrated that an ilium assigned to *Paleorhinus* by Lees (1907) actually pertains to the rauisuchian *Poposaurus*.

Mehl (1928*b*) described a second partial skull and skeleton of *Paleorhinus* (MU 530), which he named *P. parvus*, from the Popo Agie Formation at Sage Creek in the same area of Wyoming as the type locality of *P. bransoni*. The skull and lower jaw of *Paleorhinus parvus*, which is now in three pieces, show no major differences from *P. bransoni*. Mehl (1928*b*, pp. 155–156) cited principally differences in the length of the rostrum and the degree of downward deflection of the rostral tip to distinguish *P. parvus*. However, he ignored the large size difference between the skulls of the two putative species. Colbert (1947) documented that relative rostral length is proportional to skull size in phytosaurs. In addition, the deflection of the rostral tip of the holotype skull of *P. parvus* is probably the result of post-burial deformation. Thus, we consider *P. parvus* a subjective junior synonym of *P. bransoni*.

Texas. Case (1922) named *Promystriosuchus ehlersi* for a badly fractured skull from the Tecovas Formation of Crosby County, Texas. Subsequently, Gregory (1962) included this taxon in *Paleorhinus*. '*Promystriosuchus*' differs from *Paleorhinus bransoni* in lacking a posterior squamosal hook in lateral view, but this could be the result of damage to the Texas skull. The holotype skull of *Promystriosuchus ehlersi* (UMMP V7487) is badly distorted and broken anteriorly along the midline so that, in ventral view, the right tooth row is directed ventrally, but the left tooth row is oriented laterally. Also, the lateral aspect of the left external naris is visible along the split midline of the skull. Gregory (1962, pp. 671–673) criticized Case's (1922) diagnosis of *Promystriosuchus ehlersi* in detail. We agree with Gregory (1962, pp. 672–673) that all the differences between

Paleorhinus bransoni and *Promystriosuchus ehlersi* cited by Case (1922) are either errors of interpretation or are characters now recognized as variable within phytosaur taxa. *P. ehlersi* apparently differs from *P. bransoni* in having a median narial septum which is not visible in lateral view. However, the holotype is so badly distorted and fractured that we consider *P. ehlersi* a *nomen dubium* at the species level, although its holotype clearly is a specimen of *Paleorhinus*.

Langston (1949) described *Paleorhinus scurriensis* from the Camp Springs Member of the Tecovas Formation at the base of the Dockum Group in Scurry County, Texas. The holotype (TTVP 539) is a partial skull that is similar to *P. bransoni* in having a more anterior placement of the nares than in *Promystriosuchus ehlersi*, but this is a variable feature within the genus *Paleorhinus* (Gregory 1962). Langston (1949, p. 325) used qualitative criteria to distinguish this species, including exceptionally large palatine foramina, moderately elongate posttemporal fenestrae, and dorso-ventral flattening of the skull. We do not consider these characters diagnostic, because the palate of most species of *Paleorhinus* is poorly known, fenestral shape is subject to postmortem deformation, and most *Paleorhinus* skulls are dorso-ventrally flattened. We are thus unable to diagnose *P. scurriensis* as a species separate from *P. bransoni*.

Six other undescribed skulls of *Paleorhinus* are known from Texas, one from the ?lower Tecovas of Borden County (UT 31213) and five from the lower Dockum Group of Howard County (UT 31100-453, 31100-101, 31100-239, 31100-418, 31025-172; Gregory 1962; Shelton 1984). Shelton (1984) referred all these specimens to *P. scurriensis*. However, as argued above, *P. scurriensis* and *Promystriosuchus ehlersi* are both conspecific with *P. bransoni*. Indeed, we have examined these specimens, and conclude that all the Texas *Paleorhinus* material represents one taxon, *P. bransoni*.

Arizona. A small fragment of a *Paleorhinus* skull (MNA V2698) has been collected from the Downs quarry in the lowermost levels of the Petrified Forest Member of the Chinle Formation in Apache County (Murry and Long 1989). This specimen has external nares anterior to the antorbital fenestrae, but cannot be identified beyond *Paleorhinus* sp.

New Mexico. Toepelman (1916, fig. 1) described a partial phytosaur rostrum from the Bluewater Creek Member of the Chinle Formation at Fort Wingate, McKinley County (Lucas and Hayden 1989) as ?*Paleorhinus*. However, this fragment is not diagnostic below the subordinal level (Hunt and Lucas 1989). Thus, there are no known occurrences of *Paleorhinus* in New Mexico.

Eastern USA. *Paleorhinus* has not been reported from the Newark Supergroup of eastern North America (USA and Canada). Historically, and recently, most phytosaur specimens from the Newark have been assigned to *Rutiodon*, regardless of how fragmentary the material is (e.g. Olsen 1989*a*, fig. 9.7). However, much of the Newark is Carnian in age, so it is possible that some of the fragmentary phytosaur material represents *Paleorhinus*. More complete specimens will be needed to evaluate this possibility.

Morocco

Dutuit (1977) described a nearly complete phytosaurid skull from the Argana Formation as *Paleorhinus magnoculus*. This species differs from other species of *Paleorhinus* in the enormous size of the orbits and, possibly, in the exclusion of the jugal from the antorbital fenestra.

India

Huxley (1870) used the name *Parasuchus* in a table, and this taxon was validated, and the species *P. hislopi* named, by Lydekker (1885) for fragmentary reptilian fossils from the Maleri Formation of the Pranhita–Godavari Valley. Subsequently, Huene (1940) identified one of these fragments as a basicranium of the rhynchosaur *Paradapedon*. The phytosaur specimens have since been referred to aff. *Brachysuchus maleriensis* by Huene (1940) and to *Phytosaurus maleriensis* by Colbert (1958). Gregory (1962) concluded that the type specimens of *Parasuchus hislopi* were generically indeterminate. Chatterjee (1974) designated a phytosaur rostral fragment from among the syntypes

as the lectotype of *Parasuchus hislopi*, but this specimen is generically indeterminate, and thus the taxon is a *nomen dubium*. Virtually complete skeletons of a phytosaur have been collected from the Maleri Formation, and other specimens have been obtained from the Tiki Formation of the Son–Mahanadi Valley (Chatterjee 1967, 1978). Chatterjee (1978) referred these specimens to *Parasuchus*, but we follow Ballew (1989) in assigning them to *Paleorhinus*. Although the lectotype of *Parasuchus hislopi* may be a *nomen dubium*, we provisionally use the binominal *Paleorhinus hislopi* for all relevant specimens of '*Parasuchus*' pending a restudy of all the Indian specimens. The Indian species (*P. hislopi*) apparently differs from other species of *Paleorhinus* in lacking interpterygoid vacuities in the palate.

West Germany

Kuhn (1932, 1936) erected two genera and four species of phytosaurs from the Carnian Blasensandstein at Ebrach in Franconia. These taxa, *Francosuchus broilii*, *F. latus*, *Ebrachosuchus angustifrons* and *E. neukami*, are morphologically very similar to *Paleorhinus*. Indeed, Gregory (1962) and Westphal (1976) placed these taxa in a subgenus *Francosuchus* of the genus *Paleorhinus*. Chatterjee (1978) considered the specimens Kuhn described to represent the genus *Francosuchus*, which he placed in a different subfamily from *Paleorhinus*. However, the only major difference between the Ebrach specimens and other specimens of *Paleorhinus* is rostral length (Gregory 1962). *Francosuchus broilii* was originally reconstructed with a short snout (Kuhn 1932), but Kuhn (1936, p. 65) later realised that a portion of the snout was missing. The holotypes of *F. latus* (Kuhn 1932, fig. 5) and *E. angustifrons* both lack complete rostra, but that of *E. neukami* has a very elongate rostrum (Kuhn 1936, pl. 8, 1a–e). It is principally on the basis of the elongate rostrum of *E. neukami* that Gregory (1962) and Westphal (1976) placed all the Ebrach phytosaurs in a distinct subgenus from other *Paleorhinus* specimens. However, rostral length is a variable feature among phytosaurs (Gregory 1962), and we consider it a feature of taxonomic value only at the species level. Therefore, we do not uphold separate generic or subgeneric status for *Ebrachosuchus or Francosuchus*.

Chatterjee (1978) considered *Francosuchus* to be a separate genus on the basis of the position of the external nares relative to the antorbital fenestrae, which is a variable character (Gregory 1962), and the absence of posterior squamosal processes. However, the Ebrach skulls that have undamaged posterior margins exhibit posterior squamosal processes (Kuhn 1936, pl. 8, 1a; pl. 10, 5). Thus, we believe the taxonomic disposition of the Ebrach skulls should be to consider *Paleorhinus neukami* a distinct species based on its elongate rostrum, and to refer the other nominal taxa to *Paleorhinus* sp. because they lack diagnostic features.

Kuhn (1936) established another new phytosaur taxon from Ebrach, *Ebrachosaurus singularis*, that is obviously a *Stagonolepis*-like aetosaur, as noted by Benton and Walker (1985) (compare Kuhn 1936, pl. 13, 4 with Walker 1961, fig. 16, and Kuhn 1936, pl. 11, 1–3 with Walker 1961, fig. 20a–o). Kuhn also identified a lower jaw from Ebrach as *Mystriosuchus*, a Norian genus, but this specimen is indeterminate (Gregory 1962).

In 1910, Jaekel described a phytosaur skull, supposedly from the Buntsandstein (Lower Triassic) of Bernberg, as a new genus, *Mesorhinus*. There are several problems with this taxon. The holotype was found to have a label that read *Trematosaurus* (a labyrinthodont taxon: Jaekel 1910). The specimen is undoubtedly a phytosaur, but the label with the specimen indicated that it was from the Early Triassic, whereas all other phytosaur taxa are restricted to the Late Triassic (Jaekel 1910; Gregory 1962). Also, the holotype was destroyed in the Second World War (Gregory 1962). Jaekel (1910) attempted to verify the locality data on the label by examining the matrix around the specimen and concluded that it was, indeed, from the Buntsandstein, but this cannot now be checked.

Kuhn (1961) substituted the name *Mesorhinosuchus* for *Mesorhinus* because this name was preoccupied by that of a South American fossil mammal (Ameghino 1885). Recent authors have either considered *Mesorhinosuchus* Kuhn, 1961 (= *Mesorhinus* Jaekel, 1910) a tentative synonym of *Paleorhinus* (Gregory 1962; Westphal 1976) or as indeterminate (Chatterjee 1978). *Mesorhinosuchus* is undoubtedly a phytosaur (Walker 1968, p. 11; *contra* Gregory 1962, p. 675) of *Paleorhinus*-like

morphology. It differs from all other adult phytosaurs in retaining a small pineal foramen (Jaekel 1910; Camp 1930), although the holotype of *P. scurriensis* has a shallow pit in this region (Langston 1949). *Mesorhinosuchus* is best considered as *Paleorhinus* sp. on the basis of the anterior placement of the nares. The age of the specimen must be considered indeterminate.

Austria

Huene (1939) coined the name cf. *Francosuchus trauthi* for a skull fragment of a phytosaur collected in 1905 near Lunz (about 110 km southwest of Vienna), Austria. This specimen was derived from dark gray to black shale of the lower part of the Opponitzer Schichten (Opponitzer Kalk of some authors) (Trauth 1948, p. 90). The Opponitzer Schichten of the Northern Alps are a predominantly marine-limestone unit of late Carnian (Tuvalian) age (Janoscheck and Matura 1980; H. Zapfe, written comm., 1989). The skull fragment Huene named cf. *Francosuchus trauthi* clearly pertains to *Paleorhinus* and thus establishes a link between the nonmarine occurrence of *Paleorhinus* and Triassic marine biochronology.

This skull fragment is number 1905/13 in the collection of the Naturhistorisches Museum of Vienna (a sharp resin cast is NMMNM P-12960) and was illustrated by Huene (1939, fig. 1a–c), Trauth (1948, fig. 14; pl. 12, figs 6 and 7) and Westphal (1976, fig. 7*e*). It is assignable to *Paleorhinus* because the external nares are obviously forward of the antorbital fenestae and lie on the posterior portion of the rostrum. This specimen, nevertheless, exhibits no other diagnostic characters and is here referred to *Paleorhinus* sp.

THE *PALEORHINUS* BIOCHRON

Cope (1875) first used fossil vertebrates to determine the age of red beds in the American West that we now recognize to be of Late Triassic age. Subsequently, Huene (1922*a*, 1922*b*, 1926) established a crude biochronology within these red beds, based principally on phytosaurs. Huene (1926, pp. 3, 4) noted that 'parasuchians such as *Palaeorhinus* [sic]..., having a supratemporal fenestra with a high posterior border, are relatively primitive and could not possibly be of Upper Triassic age' in contrast to phytosaurs from higher stratigraphic levels such as '?*Phytosaurus doughti*'' [sic] which he thought were of Late Triassic age.

Camp (1930), in the course of his revision of the phytosaurs, realized that Huene's two faunas were both of Late Triassic age and refined the biochronology to recognize four successive faunas. Camp (1930), like Huene (1926), realized that *Paleorhinus* is more primitive than other phytosaurs, although he failed to recognize that *Pronystriosuchus* is congeneric with *Paleorhinus*.

Gregory (1962) published the next revision of the phytosaurs, and, in a series of articles (Gregory 1956, 1969; Colbert and Gregory 1957), he outlined a worldwide biochronology for the Late Triassic based on vertebrate faunas. Gregory (1956, 1969) recognized four faunas in North America, the oldest of which was defined by the co-occurrence of the phytosaurs *Paleorhinus* and *Angistorhinus*. Gregory (1956, 1969) correlated this fauna with the Blasensandstein of Germany. Chatterjee (1978) and Ballew (1989) subsequently used the occurrence of *Paleorhinus* to correlate the Argana Formation of Morocco and the Maleri and Tiki Formations of India with the Blasensandstein.

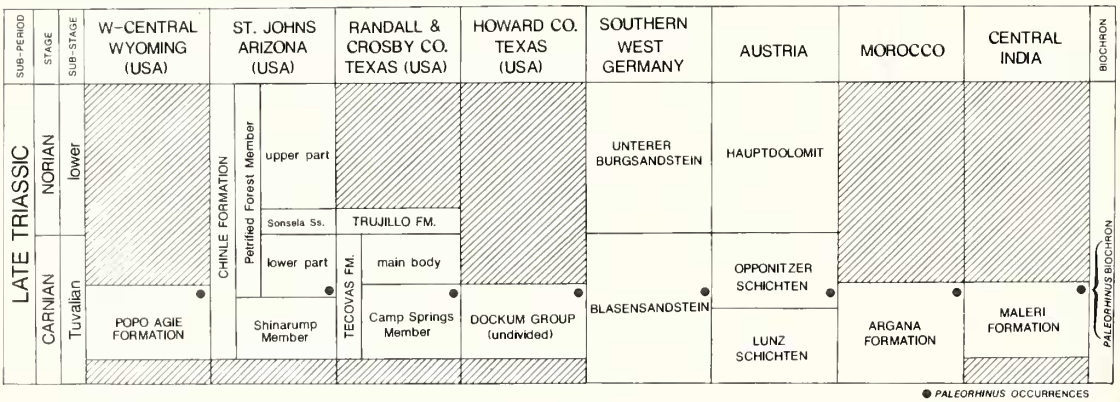
Paleorhinus occurs with faunas that are distinct from those of overlying or underlying strata and which vary geographically. The phytosaur *Angistorhinus* occurs in several faunas with *Paleorhinus* (Popo Agie, lower Dockum, Argana). The co-occurrence of the rhynchosaur *Hyperodapedon* with *Paleorhinus* in the Maleri Formation (Benton 1983) is strong evidence to suggest that the Lossiemouth Sandstone Formation of Scotland and the Wolfville Formation of Nova Scotia, which also contain *Hyperodapedon* (Benton 1983; Olsen 1989*b*), are also of the same age (*contra* Cooper 1982). A complicating factor is that the Lossiemouth fauna also includes the aetosaur *Stagonolepis* (Walker 1961; Benton and Walker 1985) which occurs in North America (*Calyptosuchus* of Long and Ballew 1985) with post-*Paleorhinus* phytosaurs (Murry and Long 1989).

The Ischigualasto Formation of Argentina and the upper Santa Maria Formation of Brazil contain the rhynchosaur *Scaphonyx* which is very similar to *Hyperodapedon* (Benton 1983) and are also probably of the same age. The Ischigualasto, Santa Maria, and Lossiemouth Sandstone Formations contain terrestrial faunas that lack semiaquatic taxa such as phytosaurs. Other tetrapod taxa that are found in *Paleorhinus*-bearing or equivalent faunas are aetosaurs (lower Dockum – *Longosuchus*; Blasensandstein – *Ebrachosuchus*; Maleri – undescribed; Ischigualasto/Santa Maria – *Aetosauroides*; Lossiemouth/lower Chinle – *Stagonolepis*), metoposaurs (Popo Agie, lower Dockum, Blasensandstein, Maleri, Argana), dicynodonts (Popo Agie, Argana, Ischigualasto), and rauisuchians (Popo Agie, lower Dockum, Maleri, Ischigualasto). Few of these taxa aid in correlation with the North American Late Triassic, but the rauisuchian *Poposaurus* occurs in the Popo Agie and the lower Dockum, and indistinguishable metoposaurs (Hunt 1989*a*) occur in the lower Dockum (*Buettneri howardensis*), Maleri (*Metoposaurus maleriensis*), Argana (*Metoposaurus azerouali*) and the Wolfville and Camp Springs (*Buettneria bakeri*: Case 1932; Baird 1986). In addition, the dicynodont *Moghreberia* from the Argana (Dutuit 1988) is very similar to *Placerias* from the lowermost Chinle (Camp and Welles 1956) and they may be congeneric (Lucas 1990). Thus, the aetosaurs, metoposaurs, dicynodonts and rauisuchians that occur in *Paleorhinus*-bearing strata or their equivalents are distinct from taxa in underlying and overlying strata.

In the western United States and Germany, *Paleorhinus*-bearing faunas are succeeded by faunas dominated by other phytosaur taxa. There are only two occurrences of overlap between *Paleorhinus* and more derived phytosaurs. At the Downs' quarry in the lower Petrified Forest Member of the Chinle Formation in northeastern Arizona, a single skull fragment of *Paleorhinus* (MNA V 2698) co-occurs with the phytosaur *Rutiodon*. The remainder of the Chinle phytosaur fauna is dominated by fossils of *Rutiodon* and *Pseudopalatus*. At Home Creek in Crosby County, Texas, Case (1922) reported the presence of *Paleorhinus* (= *Promystriosuchus*), but, subsequently, only specimens of *Rutiodon* have been found in this area (Gregory 1972). However, Case (1922) did not give exact geographic or stratigraphic information about his locality, and the *Paleorhinus*-bearing Camp Springs Member does crop out in this area (Finch and Wright 1983; Finch *et al.* 1976). Thus, the two taxa of phytosaurs may not co-occur in the same fauna in West Texas.

Paleorhinus occurs with faunas distinct from those of overlying and underlying strata that can be correlated throughout much of the world, and this taxon exhibits negligible stratigraphic overlap with other phytosaurs (Text-fig. 5). Therefore, we recognize a *Paleorhinus* biochron (Lucas and Hunt 1989) that has biochronological utility across Pangaea.

The faunas that contain *Paleorhinus* have been considered Carnian in age by all recent authors (Murry 1982, 1986, 1989; Lucas *et al.* 1985; Chatterjee 1986; Olsen and Sues 1986; Lucas and Hunt 1989; Ballew 1989). Data from palynology (lower Dockum, Blasensandstein), radiometric dating



TEXT-FIG. 5. Correlation of Upper Triassic *Paleorhinus*-bearing strata of Pangaea. See text for discussion.

(Ischigualasto) and marine invertebrates (Opponitzer Beds) have the potential of giving a more refined age for these faunas.

Paleorhinus sp. from the Opponitzer Beds from near Lunz in Austria was found associated with an upper Carnian brackish marine fauna (Huene 1939; Westphal 1976). This specimen thus can be correlated into the standard marine sequence of the Alpine province, via ammonites and pollen, that indicate it is of Tuvalian age (late Carnian: Janoscheck and Matura 1980). This ties the *Paleorhinus* biochron to Triassic marine biochronology.

The Ischigualasto Formation of the Ischigualasto–Ischichuca basin of northwestern Argentina is associated with basalt and diabases which yield radiometric ages with a mean of 224 ± 5 Ma (Gonzales and Toselli in Valencio *et al.* 1975). This date may be judged as approximately mid Carnian in age (Forster and Warrington 1985), but the spread of radiometric dates from the Ischigualasto is from early Carnian to early Norian (Forster and Warrington 1985).

The age relationships of strata of the Middle Keuper in Germany are somewhat controversial despite palynological studies (Benton 1986). The Blasensandstein, which contains *Paleorhinus*, is equivalent to part of the Rote Wand of southwestern Germany which has been considered earliest Norian or early late Carnian in age (Fisher 1972; Fisher and Bujak 1975; Kozur 1975; Gall *et al.*, 1977; Schroeder 1982). We prefer the latter correlation, as we believe that the unconformity at the base of the Stubensandstein may correlate with unconformities in other parts of the world that reflect a major eustatic fall of sea-level at the Carnian–Norian boundary (Embry 1988).

Dunay (1972) attempted to compare the palynology of the *Paleorhinus* and '*Phytosaurus*' (*Rutiodon*) zones of Gregory in the Tecovas Formation. However, Dunay's (1972) samples from the *Paleorhinus* zone were from Crosby County where, as he noted, *Rutiodon* is also found, and there are no good locality data for the older collections. Therefore, he may have sampled a *Paleorhinus* fauna, a *Rutiodon* fauna, or a transitional fauna that contains both (cf. Downs' quarry). However, Dunay (1972; Dunay and Fisher 1979) was certain that the palynofloras of the Tecovas Formation and the overlying Trujillo Formation were late Carnian in age. Litwin (1986) concluded that the lower Chinle Formation in Arizona that contains *Rutiodon*, a taxon characteristic of post-*Paleorhinus* strata in Texas, was also late Carnian in age. Palynological evidence thus suggests that the *Paleorhinus* biochron is of late-middle (middle Tuvalian), but not latest Carnian age.

Ash (1980) reviewed the biochronology of megafossil plants in North America and proposed a number of 'floral zones'. The only *Paleorhinus*-bearing stratigraphic unit that also contains megafossil plants is the Popo Agie Formation which Ash (1980) placed in his *Eoginkgoites* 'floral zone' of middle Carnian age. This age determination was based on palynological studies of the Newark Supergroup in Eastern North America (Cornet 1977) and vertebrate correlations. However, Ash (1980) only tentatively placed the Popo Agie flora in this zone, and the name-bearing taxon is only represented by ?*Eoginkgoites*. Thus, we have little confidence in assigning a middle Carnian age to the Popo Agie from the megafossil plants. Instead, we conclude that the Popo Agie is of late Carnian age.

Dutuit (1983) explained the cosmopolitan nature of Late Triassic faunas dominated by phytosaurs and metoposaurs as being due to marine dispersal by these animals. However, there is no evidence that these animals lived in marine conditions, and there are terrestrial rather than marine connections between most occurrences of these faunas (Buffetaut and Martin 1984). *Paleorhinus* was a cosmopolitan taxon in the late Carnian, but phytosaur taxa in the Norian are more restricted in their distribution (Ballew 1989). A similar situation is seen in metoposaurs (Hunt 1989*b*) and these changes reflect increased provincialization of faunas towards the end of the Late Triassic.

Acknowledgements. We thank B. Harrison (PPM) for allowing us to borrow PPM P217, R. A. Long (University of California Museum of Paleontology) for bringing some literature to our attention, H. Zapfe (Österreich Akadamie der Wissenschaft) for information about the provenance of cf. '*Francosuchus trauthi*', H. A. Kollman (Naturhistorisches Museum, Wien) for a cast of cf. '*Francosuchus trauthi*', two anonymous reviewers for their comments, M. J. Benton for editorial assistance, and the New Mexico Museum of Natural History for support.

REFERENCES

AMEGHINO, F. 1885. Nuevos restos de mamíferos fósiles oligocenos recogidos por el profesor Pedro Scalabrini y pertenecientes al Museo provincial de la cuidad del Paraná. *Boletin Academia Ciencia (Córdoba)*, **8**, 5–205.

ASH, S. R. 1980. Upper Triassic floral zones of North America. 153–170. *In* DILCHER, D. L. and TAYLOR, T. N. (eds). *Biostratigraphy of fossil plants*. Dowden, Hutchinson and Ross, Stroudsburg, Virginia, 259 pp.

BAIRD, D. 1986. Some Upper Triassic reptiles, footprints and an amphibian from New Jersey. *Mosasaur*, **3**, 125–153.

BALLEW, K. L. 1989. A phylogenetic analysis of Phytosauria from the Late Triassic of the western United States. 309–339. *In* LUCAS, S. G. and HUNT, A. P. (eds). *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History, Albuquerque, New Mexico, 414 pp.

BENTON, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London. Series B*, **302**, 605–717.

—— 1986. The Late Triassic tetrapod extinction events. 303–320. *In* PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, Cambridge, 378 pp.

—— and WALKER, A. D. 1985. The palaeoecology, taphonomy and dating of the Permo-Triassic reptiles from Elgin, northeast Scotland. *Palaeontology*, **28**, 207–234.

BUFFETAUT, E. and MARTIN, M. 1984. Continental vertebrate distribution, faunal zonation and climate in the Late Triassic. *3rd Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*, 25–29.

CAMP, C. L. 1930. A study of the phytosaurs with description of new material from western North America. *Memoirs of the University of California*, **10**, 1–174.

—— and WELLES, S. P. 1956. Triassic dicynodont reptiles. Part 1. The North American genus *Placerias*. *Memoirs of the University of California*, **13**, 255–304.

CASE, E. C. 1922. New reptiles and stegocephalians from the Upper Triassic of western Texas. *Carnegie Institution of Washington Publication*, **321**, 1–84.

—— 1932. A collection of stegocephalians from Scurry County, Texas. *Contributions from the Museum of Paleontology of the University of Michigan*, **4**, 1–56.

—— and WHITE, T. E. 1934. Two new specimens of phytosaurs from the Upper Triassic of western Texas. *Contributions from the Museum of Paleontology of the University of Michigan*, **4**, 133–142.

CHATTERJEE, S. 1967. New and associated phytosaur material from the Upper Triassic Maleri Formation of India. *Bulletin of the Geological Society of India*, **4**, 108–110.

—— 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. *Philosophical Transactions of the Royal Society of London, Series B*, **267**, 209–261.

—— 1978. A primitive parasuchid (phytosaur) from the Upper Triassic Maleri Formation of India. *Palaeontology*, **21**, 83–127.

—— 1986. The Late Triassic Dockum vertebrates: their stratigraphic and paleobiogeographic significance. 140–150. *In* PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, Cambridge, 278 pp.

COLBERT, E. H. 1947. Studies of the phytosaurs *Machaeroprosopus* and *Rutiodon*. *Bulletin of the American Museum of Natural History*, **88**, 53–96.

—— 1958. Relationships of the Triassic Maleri fauna. *Journal of the Palaeontological Society of India*, **3**, 68–81.

—— and GREGORY, J. T. 1957. Correlation of continental Triassic sediments by vertebrate fossils. *Bulletin of the Geological Society of America*, **68**, 1456–1467.

COOPER, M. R. 1982. A mid-Permian to earliest Jurassic tetrapod biostratigraphy and its significance. *Arnoldia (Zimbabwe)*, **7**, 77–103.

COPE, E. D. 1875. Report on the geology of that part of New Mexico examined during the field-season of 1874. *Annual Report of the Wheeler Survey*, 61–116.

CORNET, B. 1977. *The palynostratigraphy of the Newark Supergroup*. Unpublished Ph.D. thesis, Pennsylvania State University.

DUNAY, R. E. 1972. *The palynology of the Triassic Dockum Group of Texas, and its application to stratigraphic problems of the Dockum Group*. Unpublished Ph.D. thesis, Pennsylvania State University.

—— and FISHER, M. J. 1979. Palynology of the Dockum Group (Upper Triassic), Texas. *Reviews of Palaeobotany and Palynology*, **28**, 61–92.

DUTUIT, J. M. 1977. *Paleorhinus magnoculus*, phytosaure du Trias supérieur de l'Atlas Marocain. *Géologie Mediterranéenne*, **4**, 225–238.

—— 1983. Homogénéité et répartition des metoposauridés et phytosauridés; sont-elles en relation avec les

espaces marins du Trias supérieur? *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Série II*, **296**, 1465–1468.

—— 1988. Ostéologie crânienne et ses enseignements, apports géologique et paléoécologique, de *Moghreberia nmachouensis*, dicynodonte (Reptilia, Therapsida) du Trias supérieur marocain. *Bulletin du Muséum national d'Histoire naturelle (Paris), Serie 4*, **10C**, 227–285.

EMBRY, A. F. 1988. Triassic sea-level changes: evidence from the Canadian Arctic archipelago. *Society of Economic Paleontologists and Mineralogists Special Publication*, **42**, 249–259.

FINCH, W. I. and WRIGHT, J. C. 1983. Measured stratigraphic sections of uranium-bearing Upper Triassic rocks of the Dockum basin, eastern New Mexico, West Texas, and the Oklahoma Panhandle with brief discussion of stratigraphic problems. *United States Geological Survey Open-File Report*, **83–701**, 1–118.

—— —— and DAVIS, B. E. 1976. Unevaluated preliminary geologic cross section of uranium-bearing Upper Triassic rocks extending from Palo Duro Canyon across the Matador Arch, through the type locality of the Dockum Group, to the White River Reservoir, Crosby County, Texas. *United States Geological Survey Open-File Report*, **76–376**, 1.

FISHER, M. J. 1972. The Triassic palynofloral succession in England. *Geoscience and Man*, **4**, 101–109.

—— and BUJAK, J. 1975. Upper Triassic palynofloras from Arctic Canada. *Geoscience and Man*, **11**, 78–94.

FORSTER, S. C. and WARRINGTON, G. 1985. Geochronology of the Carboniferous, Permian and Triassic. 99–113. *In* SNELLING, N. J. (ed.). *The chronology of the geological record*. Geological Society of London, London, 340 pp.

GALL, J.-C., DURAND, M. and MULLER, E. 1977. Le Trias de part d'autre du Rhin. Corrélations entre les marges et le centre du bassin germanique. *Bulletin du Bureau de Recherches géologiques et minières*, **3**, 193–204.

GREGORY, J. T. 1956. Significance of fossil vertebrates for correlation of Late Triassic continental deposits of North America. *International Geological Congress*, **20** (2), 7–25.

—— 1962. The genera of phytosaurs. *American Journal of Science* **260**, 652–690.

—— 1969. Evolution und interkontinentale Beziehungen der Phytosauria (Reptilia). *Paläontologisches Zeitschrift*, **43**, 37–51.

—— 1972. Vertebrate faunas of the Dockum Group, Triassic, eastern New Mexico and West Texas. *New Mexico Geological Society Guidebook*, **23**, 120–123.

HUENE, F. VON 1922*a*. Neue Beiträge zur Kenntnis der Parasuchier. *Jahrbuch Preussische Geologische Landesanstalt*, **42**, 59–160.

—— 1922*b*. Kurzer Ueberblick über die triassische Reptilordnung Thecodontia. *Centralblatt für Mineralogie, Geologie und Paläontologie*, **1922**, 408–415.

—— 1926. Notes on the age of the continental Triassic beds in North America with remarks on some fossil vertebrates. *Proceedings of the United States National Museum*, **69** (18), 1–10.

—— 1939. Ein primitiv Phytosaurier in der jungeren nordostalpin Trias. *Zeitschrift für Mineralogie, Geologie und Paläontologie*, **1939**, 139–144.

—— 1940. The tetrapod fauna of the Upper Triassic Maleri beds. *Palaeontologia Indica*, **32**, 1–42.

HUNT, A. P. 1989*a*. Comments on the taxonomy of Late Triassic metoposaurs and a preliminary phylogenetic analysis of the family Metoposauridae. 293–300. *In* LUCAS, S. G. and HUNT, A. P. (eds). *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History, Albuquerque, 414 pp.

—— 1989*b*. The biochronological significance of Late Triassic metoposaurid labyrinthodonts. *New Mexico Journal of Science*, **29**, 117–118.

—— and LUCAS, S. G. 1989. Late Triassic vertebrate localities in New Mexico. 72–101. *In* LUCAS, S. G. and HUNT, A. P. (eds). *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History, Albuquerque, 414 pp.

HUXLEY, T. H. 1870. On the classification of Dinosauria, with observations on the Dinosauria of the Trias. *Quarterly Journal of the Geological Society of London*, **26**, 32–51.

JAEKEL, O. 1910. Ueber einen neuen Belodonten aus dem Buntsandstein von Bernburg. *Sitzungsberichte Gesellschaft naturforschender Freunde zu Berlin*, **5**, 197–229.

JANOSCHECK, W. R. and MATURA, A. 1980. Austria. 1–88. *In* ANONYMOUS (ed.). *Geology of the European countries*. Dunod, Paris, 433 pp.

KOZUR, H. 1975. Probleme der Triasgliederung und Parallelisierung der germanischen und tethyalen Trias. Teil II: Anschluss der germanischen Trias an die internationale Triasgliedering. *Freiberger Forschungshefte, Reihe C*, **3**, 58–65.

KUHN, O. 1932. Labyrinthodonten und Parasuchier aus dem mittleren Keuper von Ebrach in Oberfranken. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **69B**, 94–144.

—— 1936. Weitere Parasuchier und Labyrinthodonten aus dem Blasensandstein des mittleren Keuper von Ebrach. *Palaeontographica, Abteilung A*, **83**, 61–98.

—— 1961. *Die Familien der rezenten und fossilen Amphibien und Reptilien.* Verlagshus Meisenbach KG, Bamberg, 79 pp.

LANGSTON, W. JR. 1949. A new species of *Paleorhinus* from the Triassic of Texas. *American Journal of Science*, **247**, 324–371.

LEES, J. H. 1907. The skull of *Paleorhinus*. *Journal of Geology*, **15**, 121–151.

LITWIN, R. J. 1986. *The palynostratigraphy and age of the Chinle and Moenave formations, southwestern USA.* Unpublished Ph.D. thesis, Pennsylvania State University.

LONG, R. A. and BALLEW, K. L. 1985. Aetosaur dermal armor from the Late Triassic of the southwestern North America, with special reference to material from the Chinle Formation of Petrified Forest National Park. *Museum of Northern Arizona Bulletin*, **54**, 35–68.

LUCAS, S. G. 1990. Toward a vertebrate biochronology of the Triassic. *Albertiana*, in press.

—— and HAYDEN, S. N. 1989. Triassic stratigraphy of west-central New Mexico. *New Mexico Geological Society Guidebook*, **40**, 191–211.

—— and HUNT, A. P. 1989. Vertebrate biochronology of the Late Triassic. *28th International Geological Congress Abstracts*, **2**, 335–336.

—— —— and MORALES, M. 1985. Stratigraphic nomenclature and correlation of Triassic rocks of east-central New Mexico: a preliminary report. *New Mexico Geological Society Guidebook* **36**, 171–184.

LYDEKKER, R. 1885. Maleri and Denwa Reptilia and Amphibia. *Palaeontologia Indica, Series 4*, **1**, 1–38.

MATTHEWS, W. A. III. 1969. The geologic story of Palo Duro Canyon. *Bureau of Economic Geology, University of Texas, Guidebook*, **8**, 1–51.

MEHL, M. G. 1915*a*. *Poposaurus gracilis*, a new reptile from the Triassic of Wyoming. *Journal of Geology*, **23**, 516–522.

—— 1915*b*. The Phytosauria of the Trias. *Journal of Geology*, **23**, 129–165.

—— 1922. A new phytosaur from the Trias of Arizona. *Journal of Geology*, **30**, 144–157.

—— 1928*a*. *Pseudopalatus pristinus*, a new genus and species of phytosaur from Arizona. *University of Missouri Studies*, **3**, 1–22.

—— 1928*b*. The Phytosauria of the Wyoming Triassic. *Denison University Journal of Scientific Laboratories*, **23**, 141–172.

MURRY, P. A. 1982. Biostratigraphy and paleoecology of the Dockum Group (Triassic) of Texas. Unpublished Ph.D. thesis, Southern Methodist University.

—— 1986. Vertebrate paleontology of the Dockum group, western Texas and eastern New Mexico. 109–137. *In* PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic–Jurassic boundary.* Cambridge University Press, Cambridge, 378 pp.

—— 1989. Geology and paleontology of the Dockum Formation (Upper Triassic), West Texas and eastern New Mexico. 102–144. *In* LUCAS, S. G. and HUNT, A. P. (eds). *Dawn of the age of the dinosaurs in the American Southwest.* New Mexico Museum of Natural History, Albuquerque, New Mexico, 414 pp.

—— and LONG, R. A. 1989. Geology and paleontology of the Chinle Formation, Petrified Forest National Park and vicinity, Arizona and a discussion of vertebrate fossils of the southwestern Upper Triassic. 29–64. *In* LUCAS, S. G. and HUNT, A. P. (eds). *Dawn of the age of dinosaurs in the American Southwest.* New Mexico Museum of Natural History, Albuquerque, 414 pp.

OLSEN, P. E. 1989*a*. Stop 9.1: St Mary's Bay, Rossway, NS. 135–137. *In* OLSEN, P. E., SCHLISCHE, R. W. and GORE, P. J. W. (eds). *Tectonic, depositional and paleoecological history of early Mesozoic rift basins, eastern North America.* American Geophysical Union, Washington, 174 pp.

—— 1989*b*. Stop 11.1: Carrs Brook near Lower Economy. 149–150. *In* OLSEN, P. E., SCHLISCHE, R. W. and GORE, P. J. W. (eds). *Tectonic, depositional and paleoecological history of early Mesozoic rift basins, eastern North America.* American Geophysical Union, Washington, 174 pp.

—— and SUES, H.-D. 1986. Correlation of continental Late Triassic and Early Jurassic sediments and patterns of the Triassic–Jurassic tetrapod transition. 321–351. *In* PADIAN, K. (ed.). *Beginning of the age of dinosaurs: faunal change across the Triassic–Jurassic boundary.* Cambridge University Press, Cambridge, 378 pp.

SCHAEFFER, B. 1967. Late Triassic fishes from the western United States. *Bulletin of the American Museum of Natural History*, **135**, 287–342.

—— and GREGORY, J. T. 1961. Coelacanth fishes from the continental Triassic of the western United States. *American Museum Novitates*, **2036**, 1–18.

SCHROEDER, B. 1982. Entwicklung des Sedimentbeckens und Stratigraphie der klassischen Germanischen Trias. *Geologische Rundschau*, **71**, 783–794.

SHELTON, S. V. 1984. Parasuchid reptiles from the Triassic Dockum Group of West Texas. Unpublished M.Sc. thesis, Texas Tech University.

TOEPELMAN, W. C. 1916. Phytosaur remains from New Mexico. *Bulletin of the University of Oklahoma* **103**, 26–28.

TRAUTH, F. 1948. Geologie des Kalkalpenbereiches der zweiten Wiener Hochquellenleitung. *Abhandlungen der Geologie Bundesanstalt*, **26**, 1–99.

VALENCIO, D. A., MENDIA, J. E. and VILAS, J. F. 1975. Paleomagnetism and K–Ar ages of Triassic igneous rocks from the Ishigualasto–Iscichuca basin and Puesto Viejo Formation, Argentina. *Earth and Planetary Science Letters* **26**, 319–330.

WALKER, A. D. 1961. *Stagonolepis*, *Dasygnathus* and their allies. *Philosophical Transactions of the Royal Society of London*, *Series B*, **248**, 103–204.

—— 1968. *Protosuchus*, *Proterochampsa* and the origin of phytosaurs and crocodiles. *Geological Magazine*, **105**, 1–14.

WESTPHAL, F. 1976. Phytosauria. 99–120. *In* CHARIG, A. J., KREBS, B., SUES, H.-D. and WESTPHAL, F. *Thecodontia: Handbuch der Palaeoherpetologie Teil 13*. Gustav Fischer Verlag, Stuttgart, 136 pp.

WILLISTON, S. W. 1904. Notice of some new reptiles from the Upper Trias of Wyoming. *Journal of Geology* **12**, 688–697.

ADRIAN P. HUNT AND SPENCER G. LUCAS

New Mexico Museum of Natural History,
Post Office 7010, Albuquerque,
New Mexico 87194-7010, USA

Typescript received 31 January 1990
Typescript accepted 5 April 1990